ECOLOGY OF MICRO-ORGANISMS IN SOILS AS OBSERVED DURING THEIR DEVELOPMENT UPON BURIED CELLULOSE FILM

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Most soils contain an enormous population of micro-organisms, both in numbers and diversity. Among the major biological groups found in nearly all soils are bacteria, fungi, algae, Protozoa and other small fauna. There is general similarity in the populations found in different soils. With reference to bacteria, it is possible to isolate, for example, nitrifiers, nitrogen-fixers, or anaerobic spore-formers by applying the appropriate enrichment technique, from almost any soil. Similarly, amongst the fungi, many genera may be isolated readily from a great diversity of soil types. All this population is supported through the decomposition of a variety of different kinds of organic matter, and so a knowledge of the fate of the organic matter should assist in following the disposition of the micro-organisms on it.

Aerobic decomposition of fresh organic matter, such as, for example, leaf tissues, follows a course which may be divided into two phases. The first is its conversion to humus, and the second is the breakdown of the humus to simple gaseous and mineral constituents. Considered as a physical substrate, humus is organic matter which has become so extensively decomposed that it has lost all its original structure, become broken up and dispersed amongst the mineral particles of the soil. It has originated in two quite distinct ways, from synthesis of microbial tissues and metabolic products, and by accumulation of the components of the organic matter that are decomposable with difficulty. During its formation there has been a loss of carbon as carbon dioxide, and an adjustment of nitrogen content to give a carbon-nitrogen ratio (for arable soils in general) of approximately ten to one. Some mobilization of mineral constituents has also probably occurred. The rate of decomposition slows down at about the humus stage, for reasons which are not known. Further breakdown to simple products continues over a long period.

These two phases coincide with Winogradsky's (1925) division of the soil microflora into autochthonous (indigenous) and zymogenous (fermentative) flora. The former are those micro-organisms always

numerous in soil and not fluctuating much in numbers, carrying on activities which require no nutrients or sources of energy other than those normally present in soil. Soil in this context excludes organic matter which has not been humified. Winogradsky's zymogenous flora consists of those micro-organisms, developing rapidly on freshly added organic matter, which are normally present in low numbers, and to which they subside after a period of great activity.

Winogradsky regarded the autochthonous flora as primarily small coccoid bacteria, which Conn (1948) considers to be stages in the life cycle of certain normally rod-shaped bacteria, his genus *Arthrobacter*. Conn himself regards as autochthonous forms certain bacteria which are difficult to classify on account of their weak fermentative ability, chiefly non-sporing rods which either have a micrococcus stage in their life cycle (*Arthrobacter*) or remain as short rods (*Agrobacterium* Conn).

Conn regards as zymogenous micro-organisms the rest of the non-spore-forming bacteria, the spore-forming bacteria, the actinomycetes and fungi. In soil containing no fresh organic matter, the last three groups probably exist as spores, whilst the numbers of the non-spore-forming bacteria drop to a very low level, requiring special enrichment techniques to detect them.

All the soil microflora except certain non-spore-forming bacteria are therefore regarded as being responsible for decomposition of organic matter before the humus stage. Dr Garrett envisages a colonization, exploitation and exhaustion of such substrates, during which a succession of micro-organisms develops upon them. He points out that analogies can be drawn between the ecology of higher plants and the microbial ecology of soil, but with the fundamental difference that the microbial succession depletes the capacity of the habitat rather than building it up, so that the end-point of a succession of micro-organisms on a substrate is not a persisting climax association, but zero (Garrett, 1955).

Direct experimental evidence for these successions is lacking, chiefly for technical difficulties of demonstration. Indirect evidence, in the constant presence in soils of the very diverse microflora (and fauna), supports the view that particular substrates are colonized by particular micro-organisms; otherwise one would expect that in a permanent habitat such as soil the most efficient micro-organisms would have by now driven out those less efficient in decomposition of 'organic matter' and become established as a relatively small group. And since a substrate is changed by the development of micro-organisms on it, any one substrate may be expected in the course of time to provide a series of microhabitats.

It is in the study of the interrelations of micro-organisms in particular habitats that soil microbiology should be especially able to contribute to a knowledge of microbial ecology, because any substrate put into the soil will be, in the presence of an almost unlimited potential of microbial species. Those developing on it will possess certain properties. They must first be susceptible to stimulation to germinate from a resting stage. They must after germination be able to coexist with any other organism which develops at the same time or soon afterwards—perhaps having been stimulated to germinate by the development of the first organism. When the substrate has become exhausted, the organism must be able to form a resting stage to continue the species.

In this contribution, organic matter is represented by Cellophane, the brand of regenerated cellulose film made by the British Cellophane Company. It has two most suitable properties. It is a relatively pure form of cellulose, and it provides perfect conditions for observation. Simply by mounting small pieces on glass cover-slips with distilled water it is possible to observe the process of decomposition to a very advanced stage. It provides a theatre on which the course of life under soil conditions may be watched and the chief characters become known.

Cellophane has been used in order to trap soil chytrids (e.g. Haskins, 1946), but seems not to have been used before in studies on general microflora. Cellulose in the form of filter paper adhering to microscope slides and buried in forest soils was used by Cholodny (1930) in a few observations, but he never followed it up. The Cholodny slide is a glass microscope slide buried in soil, removed after a period of time, cleaned of major soil particles and stained. Since no nutrient is contained in the glass, development of micro-organisms on it is supported by organic matter in the soil. The slide reflects this development in soil organic matter rather than creating its own special habitats.

TECHNIQUE

The technique as finally adopted was as follows: British Cellophane Company P.T. 300 sheet Cellophane* was cut into pieces approximately $1{\cdot}0 \times 0{\cdot}5$ cm. and these were boiled in a large volume of distilled water to dissolve out plasticizers. After washing in another volume of distilled water they were placed singly on $\frac{7}{8}$ in. square cover-slips, the excess water was drained off and the cover-slips buried vertically in pots of soil. If the Cellophane pieces are not supported on cover-slips, it is not usually possible to recover them after about one month. The moisture

* Kindly given by British Cellophane Ltd., Bridgwater, Somerset.

holding capcity (m.h.c.) of the soil having previously been determined, the soil was watered to 60 % of this value (after adding the cover-slips). The pots were kept at laboratory temperatures and allowed to dry out to 30–40 % m.h.c., after which they were rewatered to the original value of 60 % m.h.c. The cycle lasted about 2–4 days and ensured aeration of the soil. These moisture and temperature relations were considered to give temperate conditions which would be favourable for aerobic decomposition.

The slips were dug out and examined from time to time and permanent microscope slides made by placing the cover-slip with adherent Cellophane into picronigrosin in lactophenol (Smith, 1954) for several hours, followed by washing in lactophenol. The back of the cover-slip was then washed in water, dried, and the cover-slip mounted Cellophane side downward in lactophenol on a slide. The mount was sealed with colourless nail varnish.

Before preservation the slips were examined wet under the microscope, when fungal spores could be transferred to agar plates with fine needles. Cellophane pieces were also cut up into small fragments and plated in order to examine the growing out of certain mycelia, or brushed free of surface mycelium and then cut up to obtain cultures of fungi which produced 'rooting branches' in the thickness of the Cellophane. Originally cultures of these were obtained by placing a triple 'sandwich' of Cellophane into soil, i.e. three pieces pressed together damp. After development of the fungi, the two outer pieces were removed and the 'roots' were found almost in pure culture in the centre piece. Pl. 1, fig. 1, was taken from a centre piece made in this way. Particular care was taken to ensure that the development of cultures from these sources was checked microscopically, since unwanted colonies can rapidly grow out from tiny soil particles which it is difficult to avoid transferring to the agar plate. Using filtered agar the inocula could be observed through the back of the Petri dish under $\frac{2}{3}$ in. objective, provided the dishes were not too full of agar.

SOILS

Some study has been made of Cellophane buried in the following soils:

(1) Black fen peat from an arable field near Stretham, Cambs, pH 7·0.

(2) Calcareous loam from a field near Cambridge, pH 7·2.

(3) Loamy sand from the University Farm, Cambridge, pH 6·8.

(4) Weathered chalk, from the side of a quarry near Cambridge, pH 7·6.

(5) Leaf litter taken from under firs at Santon Downham in the Breckland, Suffolk, pH *c.* 5·2.

(6) Acid sandy soil underlying the litter, pH *c.* 4·4.

With the exception of the Breckland soils these were put through a 3 mm. sieve. The larger pieces of debris were removed from the litter to obtain a uniform material, and the acid sand, being almost free of debris, was not treated.

OBSERVATIONS

In outline, the course of decomposition was similar in all the soils. Fungi were nearly always the first colonizers and after a time they became replaced by bacteria. Sometimes fungi, bacteria and residual Cellophane were consumed by soil fauna, some of which left characteristic excremental pellets which were very persistent.

In the first four soils, similar fungi developed. A few days after addition of the Cellophane, fungus hyphae begin to grow and large parts of the Cellophane are quickly covered by mycelium. Several species put characteristic 'rooting' or nutritional branches into the thickness of the Cellophane. These 'roots' support the superficial mycelium. They spread out to a limited extent and sometimes dissolve out definite cavities (Pl. 1, fig. 1) but more usually enzymic action is restricted and no cavity can be seen (Pl. 1, fig. 2). After some time 'rooting' branches may autolyze, leaving patches of Cellophane full of holes (Pl. 1, fig. 3), or they may persist, perhaps increase in extent and degenerate slowly without leaving cavities. The 'rooting' fungi which have so far been found on Cellophane in these soils belong to the genera *Botryotrichum*, *Chaetomium* (?), *Humicola*, *Stachybotrys* and *Stysanus*. Other 'rooting' fungi occur which give rise to nothing more than sterile mycelium when isolated on to Czapek-Dox or potato-dextrose agars. Other fungi which develop vigorously on Cellophane are species of *Aleurisma* (and probably *Sporotrichum*) and an oval-spored fungus which has not so far been identified. Chytrids often occur in the early stages, especially in the loamy sand soil (Pl. 1, fig. 4). They cause an intense local solution of Cellophane, but since their powers of linear extension are limited, they are not a major factor in its degradation. Secondary infection by chytrids is not usual, although they produce sporangia and zoospores *in situ*. This is probably because the Cellophane is usually extensively colonized by other fungi by the time the zoospores are liberated.

Of the filamentous fungi which begin invasion of the Cellophane, probably the commonest is *Botryotrichum piluliferum* (Sacc. & Marsh),

which is synonymous with *Coccospora agricola* (Goddard) (Downing, 1953). It produces typical 'rooting' branches, which are difficult to differentiate from those produced by *Chaetomium* (?) and *Humicola*. Aleuriospores (chlamydospores) are produced relatively late. The fungus therefore appears as a sterile mycelium on the Cellophane and has to be isolated for proof of identity.

An almost equally common isolate is a fungus believed to be a *Chaetomium*. This grows on Cellophane as a sterile mycelium indistinguishable from *Botryotrichum*, and when isolated on to agar produces tiny microspores on tips of phialides after a few days very similar to those figured in Downing's paper on *Botryotrichum* (but which I have never found on my isolates of *Botryotrichum*). After a few weeks, some isolates produce imperfect perithecia on potato-dextrose agar. These have occasionally been found on Cellophane in weathered chalk and in loamy sand (see Pl. 2, fig. 5). Only twice have perfect perithecia been seen on Cellophane (Pl. 2, figs. 6, 7), and in neither case was it possible to germinate the spores. Colonies obtained from ascospores from a *Chaetomium* perithecium growing on filter-paper laid on top of weathered chalk resembled these isolates very closely, in form of colony, production of microspores and eventual production of imperfect perithecia. Various media, including those with added paper or straw, failed to induce proper perithecial formation in any isolate.

'*Humicola grisea* Traaen (White & Downing, 1953) is another common 'rooting' fungus found in these soils. This fungus is synonymous with several other chlamydospore-forming fungi recorded in the literature on soil fungi, viz. *Monotospora dalae* Mason, *Melanogone pucciniodes* Wollenw. & Richter, and probably *Mycogone nigra* (Morgan) Jensen and *Basisporium gallarum* Moll. It produces large chlamydospores which may appear two-celled, since they are sometimes borne on an inflated hyphal cell. The hyphae may spread some distance over the glass away from the Cellophane, giving the effect of a Cholodny slide (Pl. 2, fig. 8).

Stachybotrys atra Corda occurs more sporadically. It produces characteristic long narrow 'roots', usually with a zone of hydrolysed Cellophane surrounding the rooting hyphae, and spores on normal conidiophores in great abundance (Pl. 2, fig. 9). Sometimes it reduces the piece of Cellophane on which it is growing to a sooty mass and develops so vigorously as to extend into the neighbouring soil particles (Pl. 3, fig. 10). It is easily identified without isolation.

A species of *Stysanus* has been found as a dominant in weathered chalk. It produces 'roots' and two types of spore: an *Echinobotryum* stage (Pl. 3, fig. 11) with ovate rough spores occurs, and also typical coremia bearing slightly smaller smooth oval spores (Pl. 3, fig. 12).

After a period commonly of about 3 weeks, but which may vary from 1 week in loamy sand to 10 or more in weathered chalk, the fungus mycelium becomes moribund, staining patchily in short lengths, and the contents then disappear. A tissue of dead hyphae results and this becomes colonized by bacteria (Pl. 3, fig. 13). At about this stage the Cellophane with its microbial population may be attacked by soil animals, though this is by no means always the case. Pl. 4, fig. 14, shows a patch of Cellophane bearing mycelium and spores of *Stysanus* after 39 days' burial in weathered chalk, which has been attacked by some soil animal, probably a mite, leaving small pellets of excrement some of which consist largely of *Stysanus* spores. In one sample of fen soil, annelid worms were found devouring Cellophane. After 17 days from one to five worms were found on each of a number of Cellophane pieces, and after 46 days most of the Cellophane pieces on slips buried in these pots of soil had disappeared. No characteristic solid excremental pellets were found near the Cellophane attacked by these worms, which produced a rather ill-defined semi-liquid excretion.

Provided that there is no development of soil animals (other than nematodes, which invariably occur, often in large numbers, on Cellophane in the bacterial stage), the Cellophane remains thus for a long period of time, at least of the order of several months. The substrate, which sometimes still contains a small proportion of cellulose as shown by the chlor-zinc-iodide reaction, has become unsuitable for fungal development. Resting fungus spores are commonly present. There is one exception to the absence of fungal growth, and that is the development of nematode-trapping fungi, which occasionally flourish. Pl. 4, fig. 15, shows small trapping networks of one such fungus, probably a species of *Arthrobotrys*, growing over a background of bacterial debris —the remains of Cellophane after 70 days in fen soil. Pl. 4, fig. 16, from the same slide, shows a nematode caught by the fungus which is growing over the surface of the cover-slip away from the Cellophane.

The microflora developing on the Cellophane buried in soil from Santon Downham, in either the litter or acid sand underlying it, is quite different from the preceding. The dominant fungi are species of *Oidiodendron* (Robak, 1932; von Szilvinyi, 1940; Smith, 1946) (Pl. 5, fig. 17). All the four species known, *O. fuscum*, *O. rhodogenum* and *O. nigrum* Robak and *O. flavum* von Szilvinyi are found. They develop very strongly and after 4–6 weeks may cover the Cellophane with masses of spores. Occasionally *Penicillium* spp. have been found and *P. spinulosum* Thom.

has been seen sporing. *Trichoderma* has been isolated twice from Cellophane. Actinomycetes (*Streptomyces* spp.) sometimes occur in small colonies in the earlier stages of decomposition in these soils, producing characteristic spirals of spores.

Bacterial development is less than in the neutral soils, and only occasional nematodes are found. Both fungi and Cellophane may be heavily attacked by mites. Pl. 5, fig. 18, shows Cellophane after 12 weeks' burial in litter. It has been totally destroyed, and among masses of *Oidiodendron* spores can be seen the mite pellets. The brown portions of the conidiophores scattered amongst the debris are relatively resistant to mite action. One of the mites responsible is shown in Pl. 5, fig. 18, with pellets visible inside. Pl. 5, fig. 19, shows a piece of Cellophane after 23 weeks in acid sand. All of it has been converted into mite pellets which can be seen adhering to sand grains. Slight aggregation of sand grains on to the cover-slip results from the presence of the pellets, which may be regarded as approaching the humus end of organic matter decomposition. Pl. 6, fig. 20, shows in more detail the coating forming on a sand grain. The pellets contain *Oidiodendron* spores, pieces of conidiophores and what seem to be very small bacteria, plus structureless material. Pl. 6, fig. 21, is an oil immersion photomicrograph of pellets in Pl. 5, fig. 19.

DISCUSSION

Decomposition of Cellophane pieces has been followed in a few diverse soil types under temperate conditions up to an advanced stage. There were two main phases, a fungal phase lasting perhaps from 1 to 10 weeks followed by a bacterial phase which continues indefinitely. Once the fungi had died down, they never reappeared as colonizers of the residue even after growth (and probably death of some) of the bacteria. This observation is in line with the general experience of the difficulty of demonstrating fungal hyphae growing through soil—soil being thought of in this connexion as being without unhumified organic matter.

During the fungal phase the different species often co-existed with one another. Sometimes one species would become the sole dominant, growing quickly and excluding others, such as *Stachybotrys* on the Cellophane in fen soil illustrated in Pl. 3, fig. 10; this, however, was an isolated occurrence. No evidence of antibiosis was seen. No zones of inhibition were found anywhere. The species isolated belonged to genera not noted for antibiotic production, with the possible exception of *Chaetomium*; from this genus one antibiotic has been recorded, chaetomin from *C. cochliodes* (Waksman & Bugie, 1944). In loamy

sand, there sometimes appeared to be an absence of the 'rooting' fungi from the immediate neighbourhood of a Cellophane piece, and bacteria (sometimes along with chytrids) were then responsible for its initial colonization. Bacteria were nearly always present in the fungus phase, although they were not dominant, nor responsible for much decomposition.

When the fungus hyphae died, there developed a large bacterial population, often accompanied by many nematodes. Can this be regarded as an early humus stage, with a flora of autochthonous bacteria? It is highly persistent, lasting in some soils up to 8 months at least. Cellophane itself will contribute nothing to humus, being homogeneous and readily decomposable. There appear to be several sources of soluble products at this stage, and in consequence several probable habitats for bacteria. Autolysis of fungal hyphae, and probably also of the bacteria which first develop, would release soluble products. Nematode excretions too seem to be a likely source of soluble materials. They produce no pellets of any sort and presumably their excretion is liquid. Nothing seems to be known about the physiology of nematode excretion, but being members of the animal kingdom they may be expected to excrete amounts of soluble nitrogenous compounds.

The pellets produced by soil mites may also be regarded as a form of humus. Some types of humus formed under forests in Europe are mainly composed of the excreta of soil fauna (Russell, 1950, p. 514). Subsequent decomposition of the pellets seems to be very slow.

Broad differences brought out in the different soil types were chiefly in relative length of the fungus phase. Weathered chalk and the Breckland soils had a prolonged fungus phase and few bacteria, whereas in loamy sand fungi were not always the initial colonizers.

This study has been a survey of possibilities and was not planned to be quantitative. For a quantitative estimate of the fungi which produce no characteristic structures on Cellophane with constancy, isolation into culture is necessary. Some fungi can be detected on any slide; *Stachybotrys* for example, produces its conidiophores and conidia on Cellophane buried for periods as short as 9 days, and the heavy brown conidiophores and spores persist almost indefinitely. *Stysanus* produces spores of the *Echinobotryum* type from about the same time, though the first coremia have not been found before 32 days. Chytrids can be estimated in similar manner. Some indication of the frequency of these organisms can be seen in Table 1.

The chief filamentous fungi found in the neutral soils were *Botrytrichum*, *Chaetomium* (?), sterile mycelia and *Humicola*, probably in that order. The *Aleurisma-Sporotrichum* group also occurred fairly frequently

in fen soil and loamy sand, but it was not easy to say whether these were primarily cellulose-decomposing fungi or merely associated with one of the former. *Oidiodendron* was dominant in the Santon Downham soils.

It is interesting to compare these species with those recorded by Siu (1951), which is the most comprehensive study yet made on the subject. Heading the list of order of abundance of genera from 4500 isolates from exposed cotton textiles (p. 131) are *Penicillium*, *Aspergillus*, non-sporing mycelia, *Fusarium* and *Trichoderma*, which comprise over 60 % of the total. Although the four genera mentioned are the commonest soil fungi, none was either observed to spore in Cellophane buried in the neutral soils or was present as large patches of mycelium. Conversely of the genera found on the Cellophane, *Chaetomium* is recorded as providing only 2·9 % of the isolates from the textiles, *Humicola* 0·8 % and *Sporotrichum* 0·7 % with no mention of the other genera.

Table 1. *Distribution of certain fungi on Cellophane buried in a range of soil types*

Soil type	No. of slides examined	No. of slides with *Stachybotrys*	*Stysanus*	Chytrids
1. Fen	53	8	0	2
2. Calcareous loam	45	3	0	0
3. Weathered chalk	28	0	15	1
4. Loamy sand	96	6	0	54
5. Santon Downham soils	56	0	0	0

The flora found on the Cellophane in the neutral soils is much more like that recorded by Jensen (1931) from neutral soils to which filter paper and straw had been added. By plating methods he obtained *Mycogone* (= *Humicola*), *Stachybotrys*, *Coccospora agricola* (= *Botryotrichum*) and *Botryosporium*. From more acid soils he isolated *Penicillia* and *Trichoderma*. The Breckland soils with their population of *Oidiodendron* spp. may be exceptional representatives of acid soils.

SUMMARY AND PROSPECT

A technique is described and illustrated by the use of which it is possible to follow the succession of micro-organisms on a substrate from initial burial in soil to an advanced state of decomposition. The principle is that of direct microscopical observation, together with direct isolation of the dominant organisms observed.

A community of actively developing micro-organisms lives on the substrate in a soil environment. A 'normal' course of development can be studied on a chosen soil type under temperate conditions, with its

usual variations due to heterogeneity of soil. After having established this course, deviations from it in other soil types or from particular conditions of soil treatment can be followed. Further, the use of thin sections of other materials, such as wood shavings, for example, will probably stimulate development of other communities from the soil population. By variation thus of substrate, soil and conditions of soil treatment, it should be possible to accumulate information on the interrelations of quite a number of soil micro-organisms.

I wish to thank Mr E. W. Mason of the Commonwealth Mycological Institute, Kew, for identifying *Botryotrichum piluliferum* Sacc. & Marsh and *Humicola grisea* Traaen.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. Cellophane 17 days in fen soil. ×150. 'Rooting' branches of *Botryotrichum piluliferum* in the thickness of the Cellophane, with surface mycelium pulled back. Note zones of solution of Cellophane near 'roots'. (See text on p. 291.)

Fig. 2. Cellophane 7 days in calcareous loam. ×150. 'Rooting' branches of *B. piluliferum* in thickness of Cellophane. Surface mycelium pulled off. No evident zones of solution.

Fig. 3. Cellophane 16 days in loamy sand. ×150. 'Rooting' branches of a *mycelium sterilium*. Surface mycelium brushed off. Note autolysis of 'roots' leaving cavities in Cellophane.

Fig. 4. Cellophane 10 days in loamy sand. ×150. Initial colonization by chytrids.

PLATE 2

Fig. 5. Cellophane 53 days in weathered chalk. ×150. Imperfect perithecia of *Chaetomium* (?) sp. developing on edge of Cellophane.

Fig. 6. Cellophane 53 days in weathered chalk. ×150. Part of *Chaetomium* perithecium showing hairs and ascospores.

Fig. 7. Cellophane 67 days in calcareous loam. ×150. Perithecium of *Chaetomium*.

Fig. 8. Cellophane 22 days in loamy sand. ×150. Hyphae and chlamydospores of *Humicola* growing out over the cover slip from Cellophane. Note heavy bacterial development on hyphae on and near Cellophane.

Fig. 9. Cellophane 16 days in calcareous loam. ×150. Conidiophores of *Stachybotrys* with characteristic long 'roots' in the background.

PLATE 3

Fig. 10 Cellophane 23 days in fen soil. ×150. Soil particles just above Cellophane showing heavy growth of *Stachybotrys*.

Fig. 11. Cellophane 32 days in weathered chalk. ×600. *Echinobotryum* stage of *Stysanus* sp. Note absence of bacteria.

Fig. 12. Cellophane 46 days in weathered chalk. ×150. *Stysanus* coremia.

Fig. 13. Cellophane 22 days in loamy sand. ×150. Network of decayed hyphae over which bacteria are developing.

PLATE 4

Fig. 14. Cellophane 39 days in weathered chalk. ×150. *Stysanus* tissue and Cellophane consumed by soil fauna, probably mites. Note excremental pellets in which are *Stysanus* spores.

Fig. 15. Cellophane 70 days in fen soil. ×150. Nematode-trapping networks on hyphae growing over Cellophane in 'post-fungal' stage.

Fig. 16. Same slide showing nematode trapped on the cover-slip, and hyphae extending over glass away from Cellophane.

PLATE 5

Fig. 17. Cellophane 14 days in acid sand. ×150. Conidiophore of *Oidiodendron* sp. in space by sand grains.

Fig. 18. *Above:* Cellophane 82 days in litter. ×150. Total disintegration through fungus and mite action. Background of *Oidiodendron* spores, partly eaten conidiophores and mite pellets. *Below:* Mite with two pellets *in situ*.

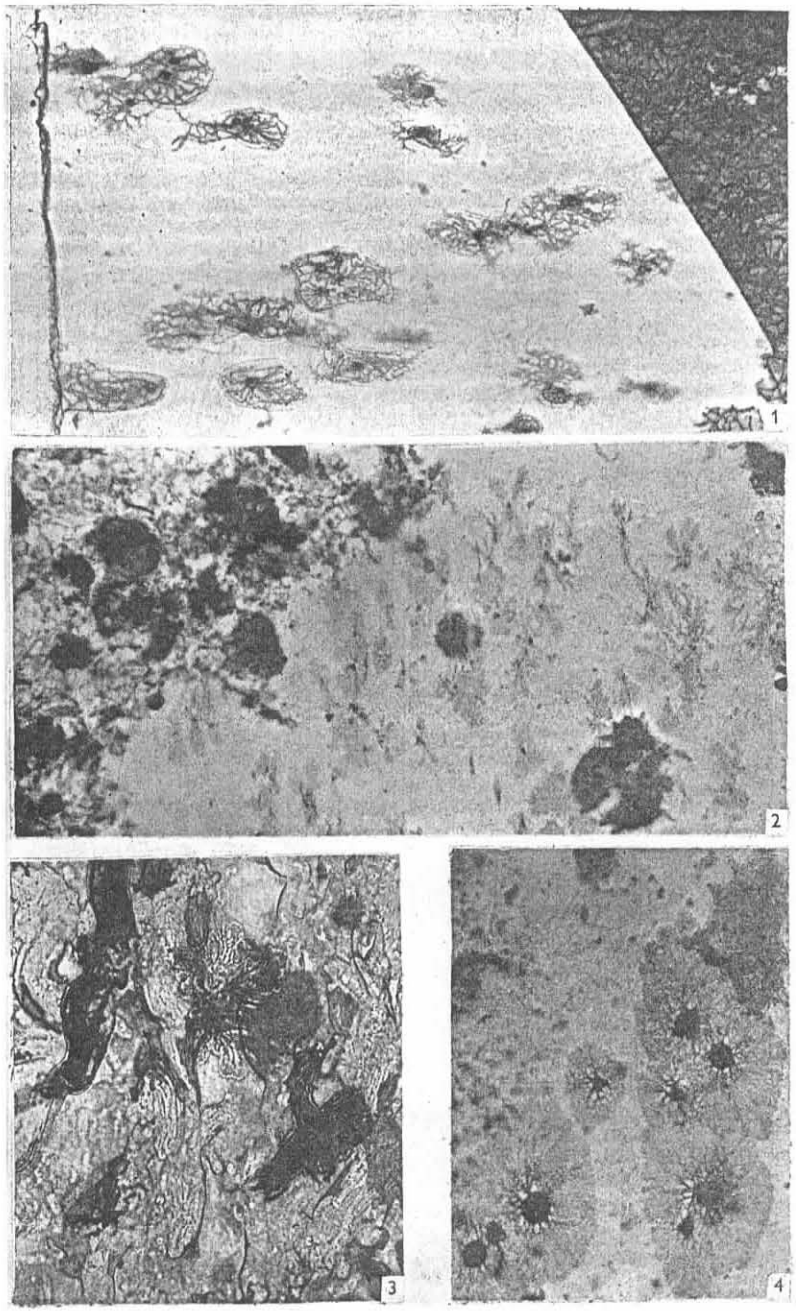
Fig. 19. Cellophane 161 days in acid sand. ×150. Total disintegration leaving pellets only, which adhere to sand grains. For *A* and *B* see Pl. 6.

PLATE 6

Fig. 20. Detail of debris coating sand grain in fig. 19 at *A*. *Oidiodendron* spores and broken conidiophores. ×600.

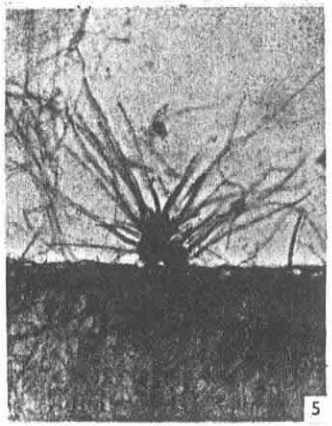
Fig. 21. Detail of pellets at *B*. *Oidiodendron* spores, pieces of conidiophore and tiny bacteria amongst amorphous material. ×1400.

PLATE I



(*Facing p.* 298)

PLATE 2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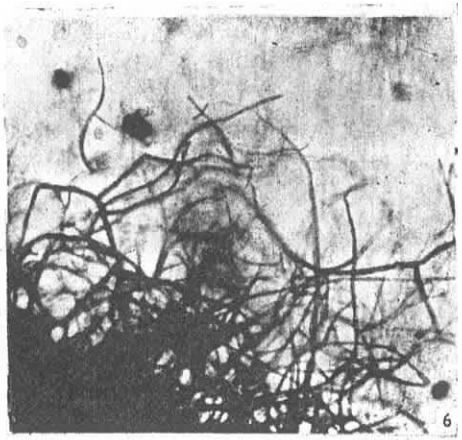
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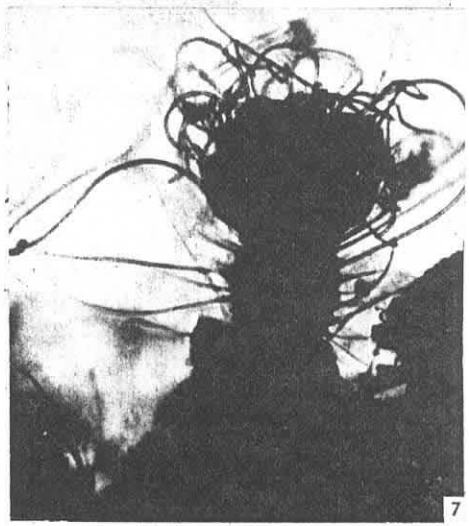
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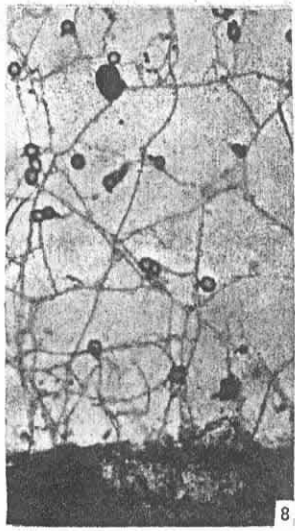
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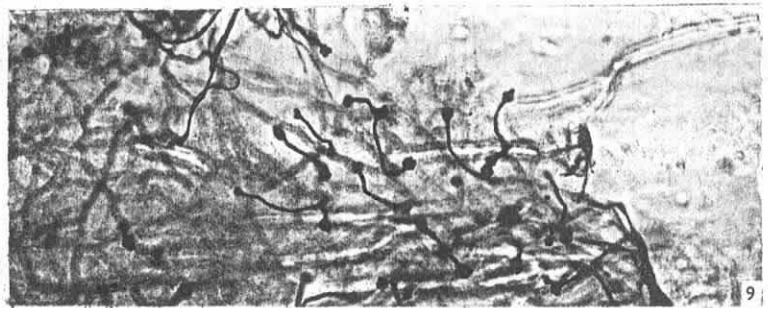
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PLATE 3

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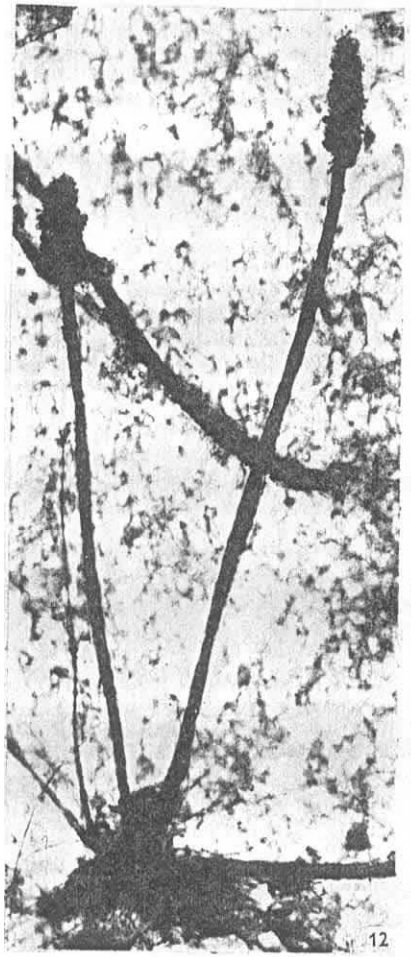
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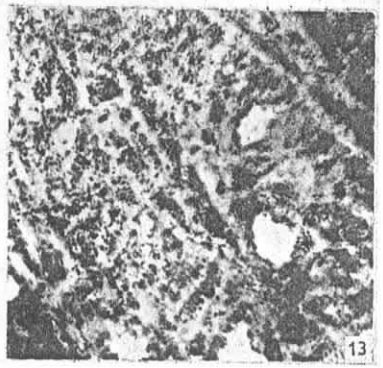
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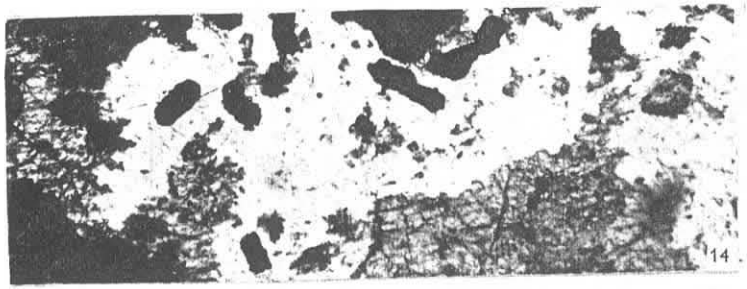
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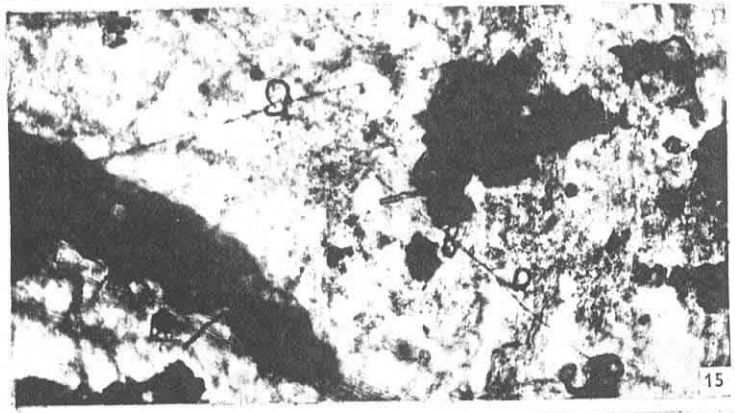
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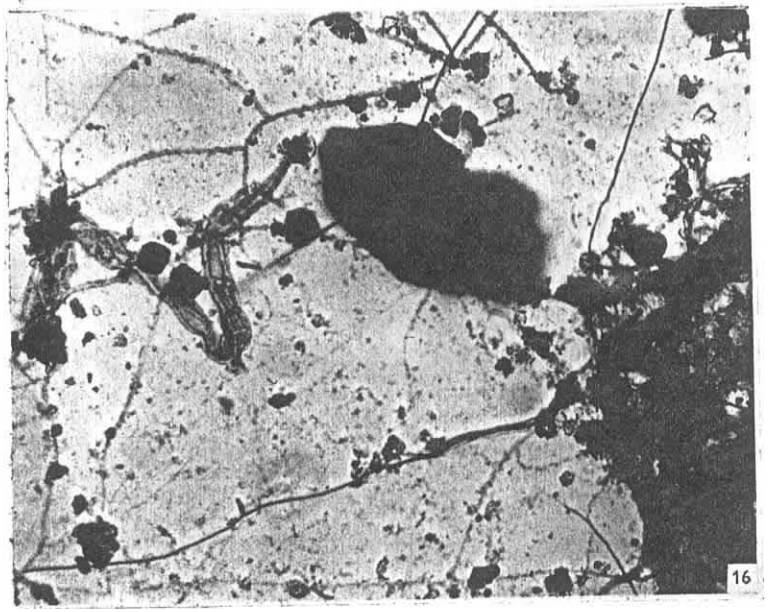
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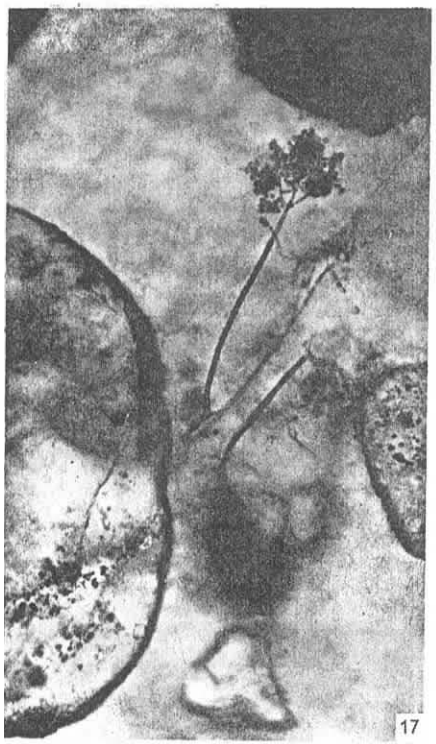
PLATE 5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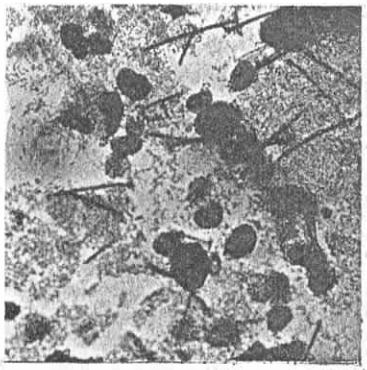

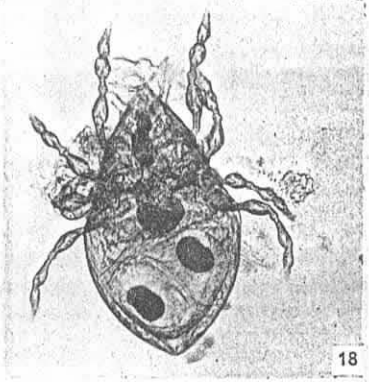
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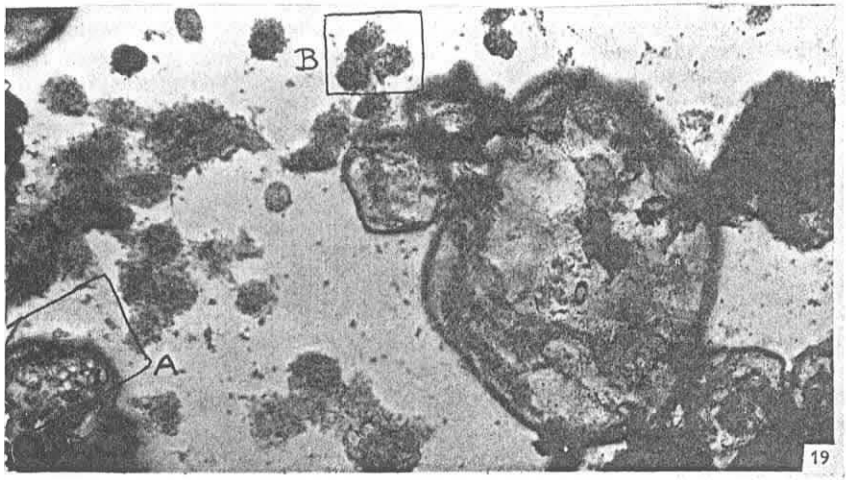

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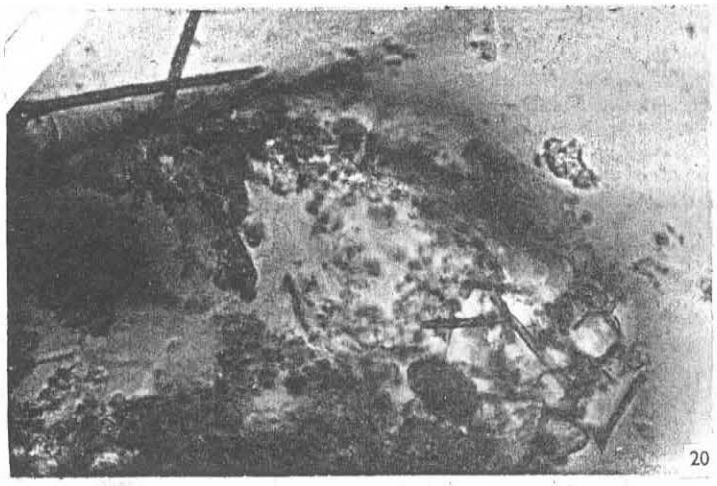
PLATE 6



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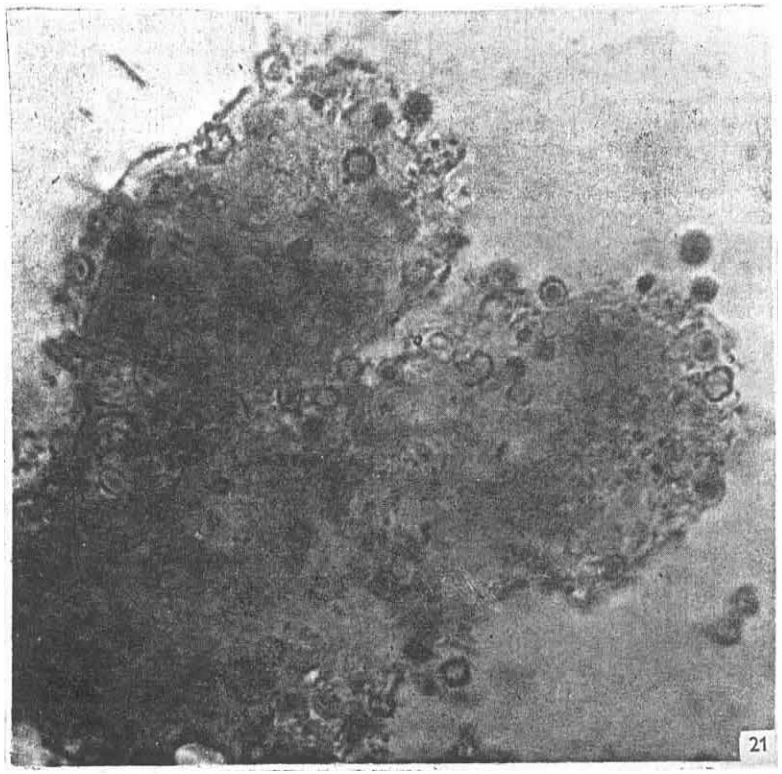

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